Inheritance of Sugarcane Borer Resistance in Sugarcane Derived from Two Measures of Insect Damage

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ABSTRACT

The sugarcane borer [*Diatraea saccharalis* (Fabricius)] is an important insect pest of sugarcane grown in the Americas. Environmental and economic concerns are driving these sugarcane industries to consider alternatives to insecticides for controlling damaging infestations of the borer. Breeding for resistance is a viable option; however, little is known of the inheritance of sugarcane borer resistance. The inheritance of sugarcane borer resistance in sugarcane (*Saccharum* spp. L.) was investigated in a field study conducted in 1990, 1992, and 1993. We measured resistance by both plant damage response ratings and mean percent internodes damaged. Seedling progeny (F_1 plants generated from seed) from 21 to 27 crosses were evaluated each year. These progeny originated from a mating design with females nested within males. Parental genotypes were randomly selected for borer resistance, but were elite cultivars adapted to Louisiana. Data were collected from progeny infested with artificially introduced sugarcane borers. Narrow-sense heritability on a single-plot basis (36 plants measured per plot) for damage ratings ($h^2 = 0.73$) and for percent damaged internodes ($h^2 = 0.76$) were high and of comparable magnitude. For both traits, we detected neither dominance nor additive × year interaction; however, dominance × year interaction variance existed. The potential for genetic advance (GA) from direct selection against percent damaged internodes (GA = 33.9% of mean bored internode) was higher than that from direct selection for lower damage rating (13.5% of mean rating). The much greater resources needed to effect selection for percent bored internodes (approx. 24 times that for rating) suggested direct selection for damage rating may be more efficient. Because the traits were highly correlated ($r_A = 0.94$) and their heritabilities high, correlated gains in percent damaged internodes by direct selection for damage rating were nearly as high as direct selection for percent damaged internodes (31% indirect vs. 33.9% direct).

The sugarcane borer is historically the most important insect pest of sugarcane in Louisiana (Long, 1969). Larval borers damage cane by boring into cane stalks were they ultimately pupate and emerge as adults. Individual larvae generally stay within a single internode. Since 1969, damaging infestations of the sugarcane borer in Louisiana have been controlled by an integrated pest management program (IPM) comprised of cultural measures, natural enemies, plant resistance, and pesticide application (Hensley, 1971). Hensley (1981) estimated that cultural controls contribute approximately 10% of season-long control, plant resistance and biological control each contribute 25%, and chemical control the remaining 40%. This pest management program has provided effective and stable control of the sugarcane borer for approximately 30 yr. Pest management programs that rely on insecticides as a principal control tactic, however, are under increasing economic and environmental pressures to reduce the IPM's dependency on insecticides.

Plant resistance may provide the additional control needed to supplant insecticides in the IPM program. Studies on plant resistance to the sugarcane borer have been published (Mathes and Ingram, 1944; Long et al., 1978). These studies have included research to determine mechanisms of sugarcane borer resistance and methods to select for resistance (Kyle and Hensley, 1970; White and Hensley, 1987). Little is known of the inheritance of sugarcane borer resistance and breeding methods required to increase resistance in clonal populations. Viator and Henderson (1971) found borer resistance to be quantitative in nature, but provided no measures of genetic variation, heritability, or potential gain from selection.

Sugarcane is a clonally propagated, out-crossing, perennial crop that growers routinely harvest once per year for about 3 yr before replanting. Ratoon crops follow the initial plant cane crop. Commercial sugarcane varieties are generated from material originally derived from interspecific crosses of sweet *noble* cultivars of *Saccharum officinarum* L. and vigorous wild relatives, principally *S. spontaneum* L. The complex polyploid nature of sugarcane commonly generates anueploids although evidence exists that commercial varieties regularly exhibit bivalent pairing (Price, 1963). These observations suggest that sugarcane acts like an allopolyploid and hence the assumption of diploid inheritance might be valid.

Quantitative studies of inheritance on sugarcane have principally focused on agronomic traits and disease resistance (Brown et al., 1968; Tai et al., 1981; Gravois et al., 1991a,b; Hogarth et al., 1983; Hogarth et al., 1993; Milligan et al., 1990; Yin et al., 1996). The objective of our study was to determine the inheritance of sugarcane resistance to the sugarcane borer employing two methods to measure insect damage. Such information will be useful in designing efficient breeding programs to increase borer resistance in sugarcane cultivars.

MATERIALS AND METHODS

This study consisted of a series of experiments conducted during the 1990, 1992, and 1993 growing seasons at the USDA-ARS, Ardoyne Research Farm near Chacahoula, LA. We used a parental population of 62 elite clones that had not been selected for borer resistance but which were adapted to Louisiana conditions. The inference population was from the

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Table 1. Male and Female Parents used in crosses for evaluating inheritance of sugarcane borer resistance.

1990		1992		1993	
Female	Male	Female	Male	Female	Male
CP84-742	LCP 82-89	HoCP85-857	CP 70-321	HoCP85-829	CP 70-330
CP 70-330	LCP 82-89	CP 84-742	CP 70-321	HoCP87-644	CP 70-330
HoCP86-973	LCP 82-89	CP 82-550	CP 70-321	US 90-25	CP 70-330
HoCP85-834	IAC 50-134	LCP 86-454	CP 70-321	CP 81-332	CP 76-331
HoCP 85-845	IAC 50-134	LCP 86-426	CP 70-321	CP 84-726	CP 76-331
HoCP85-861	HoCP85-834	CP 74-383	CP 72-356	HoCP86-924	CP 76-331
LCP 85-384	HoCP85-834	LCP 84-280	CP 72-356	LCP 87-472	CP 76-331
HoCP86-929	HoCP85-830	LCP 84-262	CP 72-356	CP 82-559	CP 83-632
HoCP86-916	HoCP85-830	CP 83-646	CP 76-331	HoCP86-916	CP 83-632
LCP 84-222	CP 84-742	CP 84-726	CP 76-331	LCP 82-89	CP 83-632
HoCP85-830	CP 84-742	CP 81-332	CP 76-331	CP 65-357	CP 83-657
LCP83-137	CP 83-657	CP 65-357	CP 83-657	CP 82-550	CP 83-657
CP65-357	CP 83-657	LCP 82-89	CP 83-657	CP 79-348	HoCP85-830
LCP 82-89	CP 70-321	HoCP85-866	HoCP85-830	HoCP85-845	HoCP85-830
HoCP86-946	CP 70-321	HoCP85-845	HoCP85-830	US 90-18	HoCP85-830
CP 72-370	CP 76-331	HoCP88-748	HoCP85-830	HoCP85-861	LCP 85-834
CP 83-606	CP 76-331	LCP 84-222	HoCP85-834	LCP 84-222	LCP 85-834
CP 84-726	CP 76-331	HoCP85-861	HoCP85-834	CP 70-321	LCP 85-384
CP 81-332	CP 76-331	HoCP86-974	HoCP85-834	HoCP87-652	LCP 85-384
HoCP85-800	HoCP85-857	HoCP85-834	IAC 50-134	HoCP88-755	LCP 85-384
HoCP86-941	HoCP85-857	HoCP85-845	IAC 50-134	HoCP87-618	LCP 86-454
		LCP 81-10	LCP 82-89	HoCP89-884	LCP 86-454
		CP 79-318	LCP 82-89	LCP 85-358	LCP 86-454
		US 90-16	LCP 82-89	US90-20	LCP 86-454
		HoCP86-917	LCP 82-89	US 80-1827	US 90-17
		HoCP86-929	LCP 84-222	HoCP85-830	US 90-17
		HoCP86-916	LCP 84-222	HoCP89-846	US 90-17

Louisiana cultivar development breeding population for commercial cultivars (Table 1). Each year, we tested (F_1) progeny populations from nine genotypes used as males that had been crossed with two to five unrelated genotypes used as females. Fifty-five different female genotypes were used during the study. Some genotypes were used as both males and females. Each year progeny from 21 to 27 biparental crosses were arranged by family and analyzed using a nested mating design model (Design 1) (Comstock and Robinson, 1948; Nyquist, 1991, p. 271). The crosses were either made the year previous to planting or were crosses made during earlier crossing campaigns and the seed stored at −18°C. Parents were not inbred.

F_1 individuals from each cross were germinated in a greenhouse in January and February and transplanted to the field during April in a randomized complete block design with four blocks. Specific progeny genotypes were tested for only 1 yr. Approximately 36 seedlings from each family were planted in a single-row plot with an intra-row plant spacing of 45 cm and an inter-row spacing of 1.8 m. Progeny were planted in a two to one skip-row configuration; two rows of cane to one row of maize (*Zea mays* L.). Infested maize rows were interspersed among the cane rows to act as spreader rows. Maize was planted at the same time as the cane and served as a host for artificial inoculation with sugarcane borer larvae. Maize was drilled and later thinned to a density of 23 000 plants ha^{-1} (4.2 plants m^{-1} row). Approximately 20 d after planting, individual maize plants were infested with 10 ± 2 neonate sugarcane borer larvae, a procedure that has proved dependable in screening trials (White, 1993).

Standard Louisiana sugarcane cultural practices were followed for cultivation, fertilization, and weed control. In addition, chlorpyrifos [*O*,*O*-diethyl-*O*-(3,5,6-trichloro-2-pyridinyl) phosphorothioate] was broadcast-applied at a rate of 1.3 kg ai ha^{-1} to control populations of the red imported fire ant, *Solenopsis invecta* (Buren). These generalized predators are effective at removing sugarcane borer, and when left uncontrolled may prevent uniform borer populations from developing in small field plots (Reagan et al., 1972).

Single stalk data were collected simultaneously at harvest (in late November or early December) and consisted of determining percent damaged internodes (single-stalk $plant^{-1}$ sample in 1990; 2-stalk $plant^{-1}$ sample in 1992 and 1993) and giving damage response ratings (single plant rating). Percent damaged internodes were measured by the ratio of bored internodes to un-bored internodes expressed as a percentage. Sugarcane typically produces 15 to 20 internodes per stalk. Stalks were not split, nor did we determine any degree of internal damage response; however, larval entrance sites are clearly identifiable following removal of leaf-sheaths. Damage response ratings were used to assess a plant's response to borer feeding. The ratings considered the production of lateral buds, and broken or dead tops in addition to the percentage of the leaf sheaths showing feeding sign prior to the larvae entering the stalk. Accumulation of frass at the leaf-sheath and reddening of the sheath are indications of larval feeding activity. Damage response ratings were based on a 1-to-9 scale, where 1 indicated little borer damage and 9 indicated heavy borer damage (Table 2).

Performing the analysis among all 3 yr and all families, we obtained restricted maximum likelihood (REML) variance

Table 2. Rating system to evaluate sugarcane borer damage.

Rating score	Description
	Resistant
1	<30% of stalks with leaf-sheath feeding
2	30 to 60% of stalks with leaf-sheath feeding
3	>60% of stalks with leaf-sheath feeding and isolated lateral shoots may be present
	Intermediate
4	<30% of stalks with lateral shoots and with or without leaf-sheath feeding
5	30 to 60% of stalks with lateral shoots and wide spread leaf-sheath feeding
6	>60% of stalks with lateral shoots and wide-spread leaf-sheath feeding
	Susceptible
7	Same as 6, and with <30% of stalks with dead or broken tops
8	Same as 6, and with 30 to 60% of stalks with dead or broken tops
9	Same as 6, and with >60% of stalks with dead or broken tops

and covariance components using the random model (Proc Mixed; SAS, 1996):

$$D_{ijklm} = \mu + Y_i + B(Y)_{ij} + M_k + F(M)_{kl} + MY_{ik} + F(MY)_{ikl} + B(MY)_{ijk} + B(FMY)_{ijkl} + \in_{ijlkm}$$

where D_{ijklm} is the response of Plant m in Year i of Block j of Male k and Female l, μ is the overall mean, Y_i is Year i effect, $B(Y)_{ij}$ is Block j in Year i effect, M_k is Male k effect, $F(M)_{kl}$ is Female l within Male k effect, MY_{ik} is interaction Male k and Year i effect, $F(MY)_{ikl}$ is Female l within Male k and Year i effect, $B(MY)_{ijk}$ is Block j in Year i and Male k effect, $B(FMY)_{ijkl}$ is Block j in Year i, Male k, Female l, and Year i effect, $\in_{ijlkm}$ error term, i.i.d. $N(0, \sigma^2_{\in})$.

Additive (σ^2_A) and dominance (σ^2_D) genetic variance were estimated as $\sigma^2_A = 4\sigma^2_M$ and $\sigma^2_D = 4(\sigma^2_{FM} - \sigma^2_M)$. We estimated narrow-sense heritability as:

$$h^2 = 4\sigma^2_M/(\sigma^2_M + \sigma^2_{FM} + \sigma^2_{MY}/y + \sigma^2_{FMY}/y + \sigma^2_{BMY}/by + \sigma^2_{BFMY}/by + \sigma^2_{\in}/pby) = 4\sigma^2_M/\sigma^2_P$$

where b was the number of blocks, y was the number of years, p was the number of plants measured per plot, and σ^2_P was the phenotypic variance. To offer standard bases of comparisons, display relative influences of different sources of variation, and to mimic the selection approach to be used in the breeding program, we calculated three types of heritabilities: a single plant basis ($y = b = p = 1$), a single plot basis ($y = b = 1$, $p = 36$), and an entry mean basis ($y = 1$, $b = 2$, $p = 36$). Standard errors of heritabilities were calculated by Dickerson's approximation (Dickerson, 1969) i.e., std. error of the $h^2 \cong 4$(std. dev. of $\sigma^2_M)/\sigma^2_P$. The additive genetic coefficient of variation (ACV) was provided to better compare the relative genetic variation of the two damage traits. It was calculated as: ACV = 100 σ_A/mean. For the three selection scenarios (single plant, single plot and entry mean), expected GA was calculated as a percentage of the mean as GA = $100ih^2\sigma_P$/mean. A 10% selection intensity with $i = 1.755$ was used in calculations (Becker, 1984, p173).

The additive correlation (r_A) between percent bored internodes (BI) and the damage ratings (RATE) was calculated as (Becker, 1984, p118):

$$r_A = \sigma_{A-BI,RATE}/[(\sigma^2_{A-BI})^{1/2}(\sigma^2_{A-RATE})^{1/2}]$$

where $\sigma_{A-BI,RATE}$ was the additive genetic male covariance of BI and RATE, σ^2_{A-BI} was the additive genetic variance for BI, and σ^2_{A-RATE} was the additive genetic variance for RATE. Expected correlated response to selection was calculated as a percentage of the mean as:

$$CR_X = 100\ i\ h_{BI}h_{RATE}r_A\sigma_{PX}/mean_X$$

where CR_X was the correlated response of Trait X to direct selection for trait Y. The square roots of the heritabilities (h_{BI} and h_{RATE}) and phenotypic variances (σ_{PX}) were used in the calculations. Two correlated responses were calculated. The expected correlated response to selection was calculated for BI (CR_{BI}) by selecting parents for RATE. Another response was figured for indirect improvement of RATE (CR_{RATE}) in progeny by selecting parents for BI.

Because sugarcane is a clonally propagated crop, a broad-sense genetic analysis is also of interest. Potential gain from clonal mass selection was compared with six selection scenarios that combined family (cross) and individual selection within families. Because of the need to estimate genetic plant-to-plant variation not confounded with nongenetic residual error variance, gain estimates were made for only bored internodes and used data from 1992 and 1993 when two stalks per plant (stool) were measured. We used progeny from families tested in all the years to obtain REML variance components from the random model:

$$D_{ijklm} = \mu + Y_i + B(Y)_{ij} + C_k + CY_{ik} + P(CBY)_{ijkl} + \in_{ijlkm}$$

where D_{ijklm} is the response of stalk m in Year i of Block j of Family k and Plant l, μ is the overall mean, Y_i is Year i effect, $B(Y)_{ij}$ is Block j in Year i effect, C_k is Family k effect, CY_{ik} is interaction Family k and Year i effect, $P(CBY)_{ijkl}$ is Plant l within Family k, Block j and Year i effect, and $\in_{ijlkm}$ error term, i.i.d. $N(0, \sigma^2_{\in})$.

We estimated GA using clonal mass selection of individuals as:

$$GA_{mass} = i\ H_{mass}\sigma_{Pmass}.$$

This assumed a 10% selection intensity from population of infinite size ($i = 1.755$), and $H_{mass} = (\sigma^2_C + \sigma^2_{PCBY})/(\sigma^2_C + \sigma^2_{CY}/y + \sigma^2_{PCBY}/pby + \sigma^2_{\in}/pbys) = (\sigma^2_C + \sigma^2_{PCBY})/\sigma^2_{Pmass}$, where $p = b = y = 1$ and stalks (s) = 2.

Expected genetic advance using combined family and individual within family selection was calculated as:

$$GA_{combined} = GA_{family} + GA_{individual} = i_f\ H_f\ \sigma_{Pf} + i_i\ H_i\ \sigma_{Pi}.$$

This assumed a 50% selection intensity among a population of 100 families ($i_f = 0.792$) and a 20% selection intensity among 125 individuals within each selected family ($i_f = 1.388$). The family heritability was calculated as

$$H_f = \sigma^2_C/(\sigma^2_C + \sigma^2_{CY}/y + \sigma^2_{PCBY}/pby + \sigma^2_{\in}/pbys) = \sigma^2_C/\sigma^2_{Pf}$$

where the number of plants (p), blocks (b), years (y), and stalks (s), varied among the six family selection scenarios. The individual heritability within selected families was estimated as:

$$H_i = \sigma^2_{PCBY}/(\sigma^2_{PCBY}/pby + \sigma^2_{\in}/pbys) = \sigma^2_{PCBY}/\sigma^2_{Pi}, \text{ where } p = b = y = 1, s = 2.$$

RESULTS AND DISCUSSION

Seven crosses were common in the 1990 and 1992 studies. Four crosses were common in the 1992 and 1993 studies. We conducted combined analyses of variance for the years 1990–1992 and 1992–1993 and analyses for individual years (analyses not shown). These analyses showed that although variability was high within a year, the σ^2_{CY} was not important, thereby, justifying the use of a pooled analysis. We assumed that including an estimate of σ^2_{CY}, poor as it may be, provided an estimate of heritability less biased than assuming no σ^2_{CY}.

Analyses showed that the male component was more important than the female-within-male component, indicating that additive variance was more important than dominance (Table 3). The standard errors associated with genetic estimates were large and can probably be attributed to the poor commonality of crosses among years and the relatively few crosses used.

Single plot heritabilities for ratings and mean percent internodes damaged were 0.73 and 0.76 (Table 3). These heritabilities are high and indicate that success in trans-

Table 3. Variance components, means, heritabilities, additive coefficient of variation (ACV), and genetic advance (GA) for sugarcane borer damage measures.

Parameter	Bored internodes	Damage rating
	—— %² ——	(rating × 10^{-2})²
σ^2_M	14.09 ± 8.40	7.09 ± 4.24
σ^2_{FM}	4.06 ± 6.27	0
σ^2_{MY}	0	0
σ^2_{MFY}	13.63 ± 6.64	7.26 ± 2.65
σ^2_{RMY}	0	1.30 ± 1.94
σ^2_{REMY}	33.20 ± 4.35	19.73 ± 2.85
$\sigma^2_{\in}$	330.27 ± 5.13	125.57 ± 1.95
σ^2_A	56.35 ± 33.60	28.34 ± 16.96
σ^2_{AY}	0	0
σ^2_D	0	0
σ^2_{DY}	54.50 ± 26.55	29.03 ± 10.58
σ^2_{ARY}	0	5.18 ± 7.75
σ^2_{DRY}	132.80 ± 17.40	73.75 ± 13.98
σ^2_P - single plant†	395.24	160.95
σ^2_P - single plot‡	74.14	38.87
σ^2_P - entry mean§	52.96	26.60
	—— % ——	—— rating ——
Mean	33.92 ± 0.23	5.89 ± 0.02
	—— unitless ——	
h^2 - single plant	0.143 ± 0.085	0.176 ± 0.105
h^2 - single plot	0.760 ± 0.453	0.729 ± 0.436
h^2 - entry mean	1.064 ± 0.634	1.065 ± 0.638
	—— % mean ——	
ACV	22.13	9.02
GA - single plant	14.66	6.65
GA - single plot	33.86	13.52
GA - entry mean	40.06	16.35

† $\sigma^2_P = \sigma^2_M + \sigma^2_{FM} + \sigma^2_{MY}/y + \sigma^2_{FMY}/y + \sigma^2_{BMY}/by + \sigma^2_{BFMY}/by + \sigma^2_{\in}/pby$ where $y = b = p = 1$.
‡ σ^2_P where $y = b = 1$, $p = 36$.
§ σ^2_P where $y = 1$, $b = 2$, $p = 36$.

ferring resistance into progeny populations should be readily possible. The importance of using multiple plants in a plot was exemplified by the dramatic increase in heritability and the doubling of the predicted genetic advance. As expected, replicating the plots further increased predicted response to selection by a smaller degree.

Previous studies indicate that damage response ratings and determining mean percent damaged internodes measure different mechanisms of resistance (White and Hensley, 1987). Ratings measure a plant's response to feeding and are, therefore, indicative of tolerance. Determination of mean percent internodes damaged measure the success of a larva in establishing itself on the plant and thus, to some degree, is a measure of antibiosis. Data reported herein show that selection for both traits is possible and advances in resistance are expected; however, the greatest GA would be expected when selecting for mean percent internodes damaged (Table 3).

The labor requirements needed to select for internodes damaged are considerably greater than collecting damage response ratings because it requires collecting stalks and removing leaf-sheaths. Evaluating tests with approximately 40 selections replicated four times by determining percent damaged internodes on the basis of 10-stalk samples requires approximately 24 laborer hours compared with1 laborer hour when visual ratings are made. Therefore, it is not always practical to obtain damaged internode data in large, segregating populations and in breeding programs initial selections are made with damage ratings (White et al., 1996).

Table 4. Correlated response to selection for percent bored internodes (BI) and damage rating (RATE) by selecting the other trait.†

	Correlated response from selecting other trait	
Selection basis	Damage rating	Bored internodes
	—— % mean ——	
Single plant	15.26	5.60
Single plot‡	30.99	12.90
Entry mean§	37.46	15.27

† Additive genetic correlation between BI and RATE was $r_{A(BI-RATE)} = 0.935$.
‡ Where years = 1, blocks = 1 and plants = 36.
§ Where years = 1, blocks = 2, and plants = 36.

The genetic correlation between these two traits was high (Table 4). Single plot correlated response to selection estimated indirect selection for bored internodes by selecting directly for resistance from ratings (31% of bored internode mean; Table 4). The expected response to selection for ratings was nearly as good as direct selection for bored internodes (34% of bored internode mean; Table 3). Given that recording bored internodes costs approximately 24 times more than damage ratings, indirect selection for bored internodes via selection based on damage ratings is well justified.

The rating system is, however, constrained from usefulness until about September because plants will not usually express damage signs such as lateral bud formation and broken tops until then. As the season progresses and the cane grows in height, the chance of lodging also increases. Thus, waiting too late in the season to rate, improves the chances of losing the opportunity to rate the plants because of lodging. Researchers commonly attempt to increase insect pressure to enhance selection of insect resistant plants. The economic threshold for borer damage in Louisiana is considered to be around 10% damaged internodes. At these levels, plant damage manifestations such as broken tops and lateral bud formation are seldom seen. Thus, the rating system has temporal and damage level constraints not experienced relative to the percent damaged internode measure.

A narrow-sense analysis provides information about potential gain from parental selection. A broad-sense analysis provides information about potential gains from clonal selection once the F_1 populations have been developed. Family selection is being used in some sugarcane cultivar development programs for yield (Cox and Hogarth, 1993; DeSousa-Vierira and Milligan, 1999; McRae and Jackson, 1995). Its utility in selecting for borer resistance has not been investigated. We compared simple mass selection (selection of individuals without reference to families) with selection approaches that combined family and individual-within-family selection. Six different family entry mean scenarios were calculated to compare the effects of different types of replication, i.e., blocking vs. number of plants vs. number stalks. The overall selection rate of 10% was maintained to compare mass selection with combined selection.

All combined selection scenarios were better than mass selection (Table 5). Combined selection increased

Table 5. Predicted broad-sense genetic advance (GA) for mass selection and family selection scenarios against percent bored internodes.

Parameter	Bored internodes
	%[2]
σ^2_C	30.5 ± 10.69
σ^2_{CY}	10.7 ± 7.11
σ^2_{PCBY}	209.8 ± 12.02
$\sigma^2_\in$	278.3 ± 8.84
	%
Mean	33.9
	% mean of
Individual GA_{mass}†	35.9
GA of combined Family (50% si) and Individual (20% si) within family selection‡	
GA Fam(p = b = y = s = 1) + GA Ind (s = 2)	42.0
GA Fam(p = b = y = 1, s = 2) + GA Ind (s = 2)	42.5
GA Fam(p = 30, b = y = s = 1) + GA Ind (s = 2)	48.5
GA Fam(p = 30, b = 4, y = 1, s = 1) + GA Ind (s = 2)	49.5
GA Fam(p = 30, b = 4, y = 1, s = 2) + GA Ind (s = 2)	49.6
GA Fam(p = 60, b = 4, y = 1, s = 1) + GA Ind (s = 2)	49.7

† σ^2_C - family, σ^2_{CY} - family by year interaction, σ^2_{PCBY} - plant within family, block and year, $\sigma^2_\in$ - residual variance.

‡ $GA_{mass} = i\, H_{mass}\, \sigma_{Pmass}$, assumes 10% selection intensity from population of infinite size, $i = 1.755$, $H_{mass} = (\sigma^2_C + \sigma^2_{PCBY})/(\sigma^2_C + \sigma^2_{CY}/y + \sigma^2_{PCBY}/pby + \sigma^2_\in/pbys) = \sigma^2_C + \sigma^2_{PCBY}/\sigma^2_{Pmass}$, $p = b = y = 1$, $s = 2$.

§ $GA_{combined} = GA_{family} + GA_{individual0} = i_f\, H_f\, \sigma_{Pf} + i_i\, H_i\, \sigma_{Pi}$, assumes 50% selection intensity among a population of 100 families, $i_f = 0.792$, and 20% selection intensity among 125 individuals within each selected family, $i_f = 1.388$, $s = 2$; $H_f = \sigma^2_C/(\sigma^2_C + \sigma^2_{CY}/y + \sigma^2_{PCBY}/pby + \sigma^2_\in/pbys) = \sigma^2_C/\sigma^2_{Pf}$ and $H_i = \sigma^2_{PCBY}/(\sigma^2_{PCBY}/pby + \sigma^2_\in/pbys) = \sigma^2_{PCBY}/\sigma^2_{Pi}$, $p = b = y = 1$, $s = 2$.

predicted gains from about 36% of the mean for mass selection to 42 to 50% of the mean, depending on the family mean scenario. Increasing the number of sampled stalks from one to two did little to increase gain, whereas increasing the number of sampled plants from 1 to 36 substantially increased gain. After increasing the number of plants to 36, replication did very little to increase predicted gain. The scenarios were chosen to illustrate differences or in some cases to provide typical mean scenarios of what might occur in the breeding program given certain production constraints. They were, however, rather arbitrarily chosen and are not construed as optimal. It seems clear that family selection promises to improve substantially the effectiveness of selection for resistance to percent bored internodes. It is assumed similar gains may be achieved for damage rating.

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